

*Journal of the Lepidopterists' Society*  
62(3), 2008, 166–170

## OLD HICKORY RECORDS AND JOHN ABBOT'S DRAWINGS: NORTH AMERICAN HOST RECORDS EVALUATED FOR *PAPILIO GLAUCUS*

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**ABSTRACT.** Accurate host plant records are an invaluable tool for anyone conducting research on the Lepidoptera. Recently, Calhoun (2007a, b) presented excellent reviews of two sets of John Abbot's butterfly life history illustrations. Within this review hickory, *Carya* sp., is identified as a host of *Papilio glaucus* (L.) based on Abbot's illustrations and records in the literature. Here we evaluate the potential for hickory, *Carya* spp., to be used as host plants by the tiger swallowtail butterflies, *Papilio glaucus* and *P. canadensis* (R. & J.). Results from larval survival and ovipositional behavior trials indicate that *Carya* spp. should not be considered hosts for these butterflies.

**Additional key words:** *Papilio*, host plant use, *Carya ovata*, *Carya laciniosa*, polyphagy, Papilionidae.

### INTRODUCTION

Fifty-four of John Abbot's life history illustrations were recently carefully evaluated by Calhoun (2007a, b). The services provided by these careful host affiliation analyses are immense for Lepidopterists, and appear accurate and logical. Nonetheless, the accuracy of one of the host plants, 'Hiccory' (*Carya* sp.) of the Juglandaceae, was assumed to have been confirmed as a host (Calhoun 2007a, b), but deserves additional analysis. There is no known convincing experimental evidence or literature verification of hickory as an acceptable/suitable host plant for the eastern tiger swallowtail butterfly, *Papilio glaucus* L. Here we evaluated hickory (2 species) as potential larval food for *P. glaucus* and *P. canadensis* (R. & J.).

The list of host plants putatively used by *P. glaucus* as a species is immense, including 17 plant families, 30 genera, and dozens of species of plants (Scudder 1888–1889; Tietz 1972; Scriber 1973, 1984; Robinson *et al.* 2002; Heppner 2003). However, many of these records are suspected to be incorrect. For example, "hop", *Humulus lupulus*, reported by Scudder (1888–1889) on the authority of J.A. Lintner as a host of *P. glaucus*, may refer to "hop tree", *Ptelea trifoliata*, which is a known host plant of *P. glaucus* (Scriber 1972). Others are a result of successive citation by more recent publications, with mistakes in larval or plant identifications inadvertently passed on as truth (Shields *et al.* 1970; Scriber *et al.* 1975). An example pertinent to the current study, is the record of *Magnolia virginiana* as a host of *Papilio palamedes* reported by Scudder (1888–1889), which is likely derived from a drawing of John Abbot's (see Calhoun 2007a, and cover of *The Journal of the Lepidopterists's Society* Vol. 61 No. 1).

This record was only recently shown to be incorrect (Scriber *et al.* 2000); as remarked by Calhoun (2006), evaluating the validity of host records from John Abbot's drawings has been complicated by the perpetuation of unconfirmed reports in the literature.

Neonate larval stages are especially critical for butterflies (Zalucki *et al.* 2002). In a test of neonate larval survival capabilities of *P. glaucus* and *P. canadensis*, Scriber (1988) evaluated 120 different plant species from 34 different families. In these analyses it was shown that *P. canadensis* could not survive on shagbark hickory, *Carya ovata* (Mill.) K. Koch (Juglandaceae), however, *P. glaucus* was not examined. Here we re-examine potential use of hickory by both butterfly species. The reported use of "Hiccory" in drawings by John Abbot was likely the original source of subsequent *Carya* sp. host plant records for *P. glaucus* reported by Scudder (1872), and subsequently by Couper (1874) and Scudder (1888–89). Scott (1986) reports *Carya* as a host for both *P. glaucus* and *P. canadensis*, but the source of this information is unclear. It therefore seems that all of these reported host records of hickory, *Carya* sp., may be traced directly or indirectly to Abbot's host entry for *P. glaucus* (Calhoun 2007a, b).

The Canadian Forest Service host records for *P. glaucus canadensis* (= *P. canadensis*) during 1947–1955 include 16 species in 6 families, but not hickory, or any other Juglandaceae species (Brower 1958). Extensive efforts to compile the host plant records for *P. glaucus* and *P. canadensis* in New York State (Shapiro 1974; Scriber 1975) and elsewhere (Scriber 1973, 1984) failed to discover any direct observations or literature records of hickory (*Carya* sp.). Recent attempts to rear neonates

of *P. canadensis* on *Carya ovata* (shagbark hickory) resulted in no survival (Hagen 1986; Scriber 1988). Black walnut (*Juglans nigra* L.; also of the Juglandaceae) also failed to support neonate larval feeding and survival of *P. canadensis* (Scriber 1988).

Here we evaluate the acceptability/suitability of two hickory species for neonates of both *P. glaucus* and *P. canadensis*; shagbark, *Carya ovata* (Mill.) K. Koch, and shellbark, *C. laciniosa* (Michx. F.) Loud. We also evaluate the willingness of *P. glaucus* females to oviposit on hickory in a multi-choice arena.

#### MATERIALS AND METHODS

##### Oviposition

Wild caught *P. glaucus* females collected in Oglethorpe County, Georgia (n=18) and St. Joseph County, Indiana (n=4) were shipped to our labs at Michigan State University. *P. canadensis* females were caught and brought directly to our labs from Charlevoix County, Michigan. Ovipositional assays followed similar procedures as those described by Scriber (1993). Females were individually placed into circular oviposition arenas which rotated in front of a 60 watt light bank. Each arena contained leaves from eight different tree species, one of which was the "Hickory" species *C. laciniosa*. The other seven types of leaves were from known host plants of *P. glaucus* and/or *P. canadensis* and included tulip tree (TT=*Liriodendron tulipifera* L., Magnoliaceae), white ash (WA=*Fraxinus americana* L., Oleaceae), black cherry (BC=*Prunus serotina*, Ehrh., Rosaceae), quaking aspen (QA=*Populus tremuloides* Michx., Salicaceae), paper birch (PB=*Betula papyrifera* Marsh, Betulaceae), hop tree, (HT=*Ptelea trifoliata*, L., Rutaceae), and spice bush, (SB=*Lindera benzoin* L. Blume, Lauraceae). The leaves were all of approximately the same size and were spaced at equal distances around the perimeter of the arena.

Butterflies were fed a honey water solution daily and allowed to oviposit until they were too weak to fly (2–5 days). The number of eggs laid on leaves of each plant or non-leaf portions were counted daily and the leaves replaced with new leaves as necessary to insure leaf quality remained high. All eggs laid on each leaf were summed across days and the data interpreted as percentages for each individual female. A small proportion of eggs laid on secondary hosts, non-hosts, and non-plant material such as the plastic sides of the arena or the paper towel lining the bottom are common in ovipositional studies of this nature. Only females that laid more than 20 eggs in the arenas were used in this study (n=7 Georgia, n=1 Indiana).

##### Larval Rearing

*P. glaucus* larval abilities were assessed using recently hatched neonates (n=144) from females collected in Oglethorpe County, Georgia (n=10 females) and St. Joseph County, Indiana (n=2 females) placed on leaves of *C. laciniosa* and *C. ovata*. To assess *P. canadensis* larval abilities, neonates from six wild caught females collected in Cheboygan County, Michigan (n=28) were put on leaves of *C. ovata*. As a control, neonates from some of the same families (*P. glaucus* fam.=5, n=39, *P. canadensis* fam.=4, n=29) were also placed on a known host plant of both swallowtail species, black cherry, *Prunus serotina* (Rosaceae) (Scriber 1988), which allowed a comparison of survival and growth rates to those of larvae on hickory. Larval survival on black cherry is known to be comparable to survival on other hosts for *P. glaucus*, including tulip tree, white ash, and hop tree (Scriber 1996). All leaves used in this study came from local areas in Ingham County, Michigan, known to be pesticide free.

The placement of neonates was done using a fine camelhair brush. From one to seven larvae were gently positioned in a paper towel-lined Petri dish along with a *C. laciniosa*, *C. ovata*, or *P. serotina* leaf (in no-choice assays). The leaves were kept moist and turgid by insertion into a water filled aquapic (Scriber 1977). Larval survival was recorded at three and six day intervals. Prior observations by us indicated that in order for a larva to survive beyond three days, it is necessary for it to feed. However, the act of feeding alone does not indicate that a plant is a suitable host for the larvae. Additionally, of those larvae that survive to pupation, we have observed that the vast majority will either have reached the second instar or will be in the act of molting into the second instar by day six.

A comparison of survival on *Carya* sp. versus *P. serotina* was made using Fishers exact test (P-value < 0.05 was considered significant). We combined the two species of hickory for this analysis as no difference was seen in larval survival on the two potential hosts.

#### RESULTS

The mean number of eggs laid by *P. glaucus* females on *C. laciniosa* was  $4.5 \pm 2.2$  % of the total (Figure 1). Ovipositional preferences were highly variable both among individual females and between females, making firm conclusions difficult. The fact that such a high proportion of eggs were laid on tulip tree and white ash (> 67% of total) may indicate that individual females were exhibiting a high degree of specificity. The proportion of eggs laid on *C. laciniosa* is comparable only to secondary and non-host plants and was never higher than a primary host plant (TT, WA, or HT).

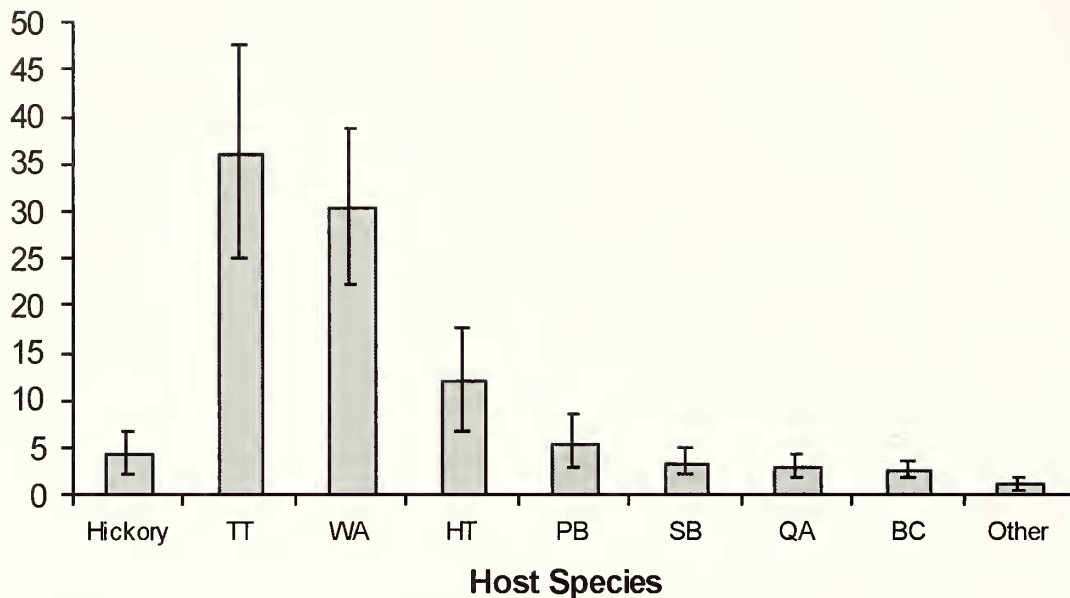


FIG. 1. Mean percent of eggs  $\pm$  SEM laid by *P. glaucus* females ( $n=7$ ) on leaves in an eight choice oviposition assay. The plant species are shellbark hickory (hickory), *Carya laciniosa*, tulip tree (TT), *Liriodendron tulipifera*, white ash (WA), *Fraxinus americana*, hop tree (HT), *Ptelea trifoliata*, paper birch (PB), *Betula papyrifera*, spice bush (SB), *Lindera benzoin*, quaking aspen (QA), *Populus tremuloides*, and black cherry (BC), *Prunus serotina*. "Other" indicates eggs laid on either the plastic sides of the oviposition arena or the paper toweling lining the bottom of the arena.

Other ovipositional studies have found similar results for the proportion of eggs laid on non-hosts and marginal hosts in our ovipositional arenas (Mercader & Scriber 2005, 2007). The results from these ovipositional profiles indicate that *Carya* spp. are unlikely to be selected for oviposition as primary hosts, but rare events might be feasible in which eggs are placed on *Carya* spp. when preferred hosts were unavailable or intermingled with leaves of a suitable host (e.g. at the edge of a forest or hedgerow).

In any case, survival by both *P. canadensis* and *P. glaucus* larvae on *Carya* sp. clearly indicate that these plants are unsuitable larval hosts. Only 18 out of 144 *P. glaucus* larvae survived for three days on *Carya* spp., and only one individual lived past six days. This individual died while molting to the second instar on the seventh day. Out of 28 *P. canadensis* larvae, only two lived past the third day and none lived to six days. By comparison, when feeding on black cherry, 27 of 29 individuals of *P. canadensis* survived to the sixth day. In addition, of 39 *P. glaucus* neonates placed on *P. serotina*, 37 individuals survived to day six. Not surprisingly, first instar survival in both *P. glaucus* and *P. canadensis* was significantly different on *Carya* spp. and *P. serotina* (Fisher's Exact Test,  $P < 0.001$ , Table 1). In this study, individuals placed on *P. serotina* were all from families also tested on *Carya* spp.

#### DISCUSSION

The reports of larval food plants for herbivorous insects have been frequently constrained in their accuracy by the ability of the observer/reporter to correctly identify the plant and/or the insect. Nowhere are such errors more likely than with polyphagous insects that feed on many species, genera, and families of plants. The eastern tiger swallowtail, *P. glaucus*, and northern (Canadian) tiger swallowtail, *P. canadensis*, are among the most polyphagous of all 560 species of Papilionidae worldwide with respect to larval host plants (Scriber 1973, 1984). Hickory species (*Carya* spp.) are shown to be unsuitable for both species, despite the early references to "Hiccorry" by John Abbot for drawings of *P. glaucus* dark morph females (Calhoun

TABLE 1. The number of larvae alive and dead after six days. Differences in survival of *P. glaucus* and *P. canadensis* larvae on *Carya* sp and a known host plant, *P. serotina*, are significant (Fisher's Exact Test,  $P < 0.001$ ).

|                    | <i>P. canadensis</i> |      | <i>P. glaucus</i> |      |
|--------------------|----------------------|------|-------------------|------|
|                    | Alive                | Dead | Alive             | Dead |
| <i>Carya</i> spp.  | 0                    | 28   | 1*                | 143  |
| <i>P. serotina</i> | 27                   | 2    | 37                | 2    |

\* This individual survived until the sixth day, but died while molting to the second instar on day seven.

2007a, b) and subsequent listings by other lepidopterists. It seems feasible that the compound leaf of an ash species (*Fraxinus* spp.) might have been mistaken by Abbot for the compound leaf of hickory ('Hicory').

It is not surprising to find additional plant species that may serve as oviposition substrates for these tiger swallowtail butterflies, but which are not acceptable/suitable hosts for the larvae (Brower 1958; Straatman 1962; Wiklund 1975; Berenbaum 1981; Scriber *et al.* 1991; Scriber 1993; Zalucki *et al.* 2002). Experiments with hybrid individuals have shown that the inheritance of traits for larval host suitability and ovipositional preference are independent of each other in several butterflies (e.g. Scriber *et al.* 1991; Forister 2005; Nygren *et al.* 2006; Scriber *et al.* 2008), which may help explain how some of the conflicts between adult host selection and larval host use ability may arise. It is feasible that such willingness to oviposit on "non-hosts" in polyphagous species may facilitate the oscillation between species-wide generalization and local specialization that could help generate new species (Thompson 1998; Nosil 2002; Janz *et al.* 2006). It has been suggested that the transitions from generalist to locally specialized forms may be accomplished by retention of the rank hierarchy but with flexibility in the "specificity" of host use (Courtney *et al.* 1989; Bossart & Scriber 1995; Mercader & Scriber 2005, 2007). Our multiple choice oviposition study, which included *C. laeiniosa* as one of eight choices, indicated that a small proportion of eggs may be laid on hickory, but the proportion of eggs laid was very low as observed for other non-hosts (Scriber *et al.* 1991; Mercader & Scriber 2005, 2007). Butterflies in our ovipositional arenas are attracted to the lighted side of the arenas and thus are presented with a different leaf as the arenas rotate, restricting any mechanistic inference (i.e. cues) to contact chemoreception. In the field it is likely that pre-alighting cues (e.g. odor or visual cues) may reduce the encounter rate with *Carya* spp., making the likelihood of these ovipositional 'mistakes' very low.

The absence of survival on *Carya* spp. found in this study for both *P. glaucus* and *P. canadensis* (Table 1) indicates that even if occasional eggs are deposited on *Carya* spp. the neonate larvae are unlikely to survive. The majority of individuals placed on *Carya* spp. did not feed, and the small proportion that did was unable to survive to the second instar. Geographic variation in preference and performance of *P. glaucus* and *P. canadensis* is known (e.g. Scriber *et al.* 1991; Bossart & Scriber 1995), and a few populations of *P. glaucus* may encounter more suitable *Carya* spp. than the ones examined here. However, despite this possibility, our

results using two species of *Carya* corroborate previous findings for *P. canadensis* (Scriber 1988) and field observations (Shapiro 1974; Scriber 1973, 1975, 1985) that *Carya* spp. are not host plants of *P. canadensis* or *P. glaucus*. While the services that have been provided by literature reviews are invaluable, the results from this study highlight the importance of verifying host use reports in order not to perpetuate errors in the literature.

#### ACKNOWLEDGEMENTS

This research was supported in part by the College of Natural Sciences, the Michigan State Agricultural Experiment Station (MAES Project # 01644), and the National Science Foundation (DEB-0716683). MA was supported by awards from the College of Natural Science and "Scriber Scholars in Butterfly Biology and Conservation". We thank James Maudsley, Carsten Nowak and Howard Romack for assistance in obtaining female *Papilio* for these studies. A previous draft of this manuscript was significantly improved by comments from J.V. Calhoun and an anonymous reviewer.

#### LITERATURE CITED

- BERENBAUM, M.R. 1981. An oviposition "mistake" by *Papilio glaucus* (*Papilionidae*). *J. Lepid. Soc.* 35: 75.
- BOSSART, J.L. & J.M. SCRIBER. 1995. Maintenance of ecologically significant genetic variation in the tiger swallowtail butterfly through differential selection and gene flow. *Evol.* 49: 1163–1171.
- BROWER, L.P. 1958. Larval foodplant specificity in butterflies of the *P. glaucus* group. *Lepid. News* 12: 103–114.
- CALHOON, J.V. 2006. A glimpse into a "flora et entomologia": the natural history of the rarer lepidopterous insects of Georgia by J. E. Smith and J. Abbot (1797). *J. Lepid. Soc.* 60: 1–37.
- \_\_\_\_\_. 2007a. John Abbot's butterfly drawings for William Swainson, including general comments about Abbot's artistic methods and written observations. *J. Lepid. Soc.* 61: 1–20.
- \_\_\_\_\_. 2007b. The butterfly drawings by John Abbot in the Hargrett Rare Book and Manuscript Library, University of Georgia. *J. Lepid. Soc.* 61: 125–137.
- COUPER, W. 1874. A dissertation on northern butterflies. *Can. Entomol.* 6: 91–96.
- COURTNEY, S.P., G.K. CHEN & A. GARDNER. 1989. A general model for individual host selection. *Oikos* 55: 55–65.
- FORISTER, M. 2005. Independent inheritance of preference and performance in hybrids between host races of *Mitoura* butterflies (*Lepidoptera*: *Lycaenidae*). *Evolution* 59: 1149–1155.
- HAGEN, R.H. 1986. The evolution of host plant use by the tiger swallowtail butterfly, *Papilio glaucus*. PhD Dissertation, Cornell University, Ithaca, New York. 297 pp.
- \_\_\_\_\_, R.C. Lederhouse, J. Bossart & J.M. Scriber. 1991. *Papilio canadensis* and *P. glaucus* (*Papilionidae*) are distinct species. *J. Lepid. Soc.* 45: 245–258.
- HEPPNER, J.B. (ed.). 2003. *Lepidoptera of Florida*. Part 1: introduction and catalog. *Arthropods of Florida and neighboring land areas*. Vol. 17. Florida Dept. Agric. Cons. Serv., Div. Plant Ind., Gainesville, Florida. 670 pp., 65 pl.
- JANZ, N., S. NYLIN & N. WAHLBERG. 2006. Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evol. Biol.* 6: 4.
- MERCADER, R.J. & J.M. SCRIBER. 2005. Phenotypic plasticity of host selection in adult tiger swallowtails; *Papilio glaucus* (L.). Pp 25–57. In T.N. Ananthakrishnan & D. Whitman (eds.), *Insects phenotypic plasticity: Diversity of responses*. Sci. Publ., Enfield, NH, USA.
- \_\_\_\_\_ & \_\_\_\_\_. 2007. Diversification of host use in two polyphagous butterflies: differences in oviposition specificity or host rank hier-

- archy? *Entomol. Exp. et Appl.* 125: 89–101.
- NOSIL, P. 2002. Transition rates between specialization and generalization in phytophagous insects. *Evol.* 56: 1701–1706.
- NYGREN, G.H., S. NYLIN, & C. STEFANESCU. 2006. Genetics of host plant use and life history in the comma butterfly across Europe: varying modes of inheritance as a potential reproductive barrier. *J. Evol. Biol.* 19: 1882–1893.
- ROBINSON, G.S., P.R. ACKEBY, I.J. KITCHING, G.W. BECCALONI, & L. M. HERNÁNDEZ. 2002. Hostplants of the moth and butterfly caterpillars of America north of Mexico. *Mem. Amer. Entomol. Inst.* 69: 1–824.
- SCOTT, J.A. 1986. *The butterflies of North America; A natural history and field guide.* Stanford Univ. Press, Stanford, California. 583 pp., 64 pl.
- SCRIBER, J.M. 1972. Confirmation of a disputed foodplant of *Papilio glaucus* (Papilionidae). *J. Lepid. Soc.* 26: 235–236.
- \_\_\_\_\_. 1973. Latitudinal gradients in larval feeding specialization of the World Papilionidae. *Psyche*, 80: 355–373.
- \_\_\_\_\_. 1975. Comparative nutritional ecology of herbivorous insects: Generalized and specialized feeding strategies in the Papilionidae and Saturniidae (Lepidoptera). PhD Dissertation, Cornell University, Ithaca, NY. 289 pp.
- \_\_\_\_\_. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). *Oecologia* 28: 269–287.
- \_\_\_\_\_. 1984. Larval foodplant utilization by the world Papilionidae (Lepidoptera): Latitudinal gradients reappraised. *Tokurana (Acta Rhopalocerologica)* 2: 1–50.
- \_\_\_\_\_. 1988. Tale of the tiger: Beringial biogeography, binomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies. Pp. 240–301. *In* K.C. Spencer (ed.), *Chemical mediation of coevolution.* Academic Press, New York, NY, USA.
- \_\_\_\_\_. 1993. Absence of behavioral induction in oviposition preference of *Papilio glaucus* (Lepidoptera: Papilionidae). *Great Lakes Entomol.* 26: 81–95.
- \_\_\_\_\_. 1996. Tiger tales: Natural history of native North American swallowtails. *Am. Entomol.* 42: 19–32.
- \_\_\_\_\_, R.C. LEDERHOUSE & L. CONTARDO. 1975. Spicebush, *Lindera benzoin* (L.), a little known foodplant of *Papilio glaucus* (Papilionidae). *J. Lepid. Soc.* 29: 10–14.
- \_\_\_\_\_, B.L. GIEBINK & D. SNIDER. 1991. Reciprocal latitudinal clines in oviposition behavior of *Papilio glaucus* and *P. canadensis* across the Great Lakes hybrid zone: possible sex-linkage of oviposition preferences. *Oecologia* 87: 360–368.
- \_\_\_\_\_, N. MARGRAFF & T. WELLS. 2000. Suitability of four families of Florida “bay” species for *Papilio palamedes* and *P. glaucus* (Papilionidae). *J. Lepid. Soc.* 54: 131–136.
- \_\_\_\_\_, G.J. ORLING, & R.J. MERCADER. 2008. Introgression and parapatric speciation in a hybrid zone. Pp 69–87. *In* K.J. Tilmon (ed.), *Specialization, speciation, and radiation: The evolutionary biology of herbivorous insects.* University of California Press, Berkeley, CA.
- SCUDDER, S.H. 1872. Abbott's [sic] notes on Georgian butterflies. *Can. Entomol.* 4: 73–77, 84–87.
- \_\_\_\_\_. 1988–1989. *The butterflies of the Eastern U.S. and Canada.* 3 Vols. Publ. by the author. Cambridge, Massachusetts. 1958 pp., 89 pl.
- SHAFFIRO, A.M. 1974. *The butterflies and skippers of New York State.* Cornell University Agric. Exp. Station Res. (Search) 4: 1–60.
- SHIELDS, O., J.M. EMMEL, & D.E. BREEDLOVE. 1970. Butterfly larval foodplant records and a procedure for reporting foodplants. *J. Res. Lepid.* 8: 20–36.
- STRAATMAN, R. 1962. Notes on certain Lepidoptera ovipositing on plants which are toxic to their larvae. *J. Lepid. Soc.* 16: 99–103.
- THIETZ, H.M. 1972. *An index to the described life histories, early stages and hosts of the Macrolepidoptera of the continental United States and Canada.* 2 Volumes. Allyn Mus. Entomol., Sarasota, Florida. 1041 pp.
- THOMPSON, J.N. 1998. The evolution of diet breadth: monophagy and polyphagy in swallowtail butterflies. *J. Evol. Biol.* 11: 563–578.
- WIKLUND, C. 1975. The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia* 18: 185–197.
- ZALUCKI, M.P., A.R. CLARKE & S.B. MALCOLM. 2002. Ecology and behavior of first instar larval Lepidoptera. *Ann. Rev. Entomol.* 47: 361–393.

*Received for publication 9 November 2007; revised and accepted 28 May 2008.*